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HEMISPHERIC EQUIPOTENTIALITY

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SAMUEL A. KIRK

A DISSERTATION

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR
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HEMISPHERIC CEREBRAL DOMINANCE AND HEMISPHERIC EQUIPOTENTIALITY ^{1,2}

A STUDY OF THE EFFECTS OF UNILATERAL CORTICAL LESIONS ON HANDEDNESS, PATTERN VISION, AND INTELLIGENT BEHAVIOR IN THE ALBINO RAT

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The theory of cerebral dominance assumes that the functions of handedness, speech, reading, and even memory, volition, intelligence, and personality are activities of one cerebral hemisphere: the left in right-handed individuals and the right in left-handed individuals. This theory is not based on experimental evidence but is suggested by the preferential use of one hand and by sporadic clinical or neuropathological cases. It assumes that cerebral lesions in the dominant hemisphere result in various psychological disturbances, whereas lesions in the non-dominant hemisphere do not result in these disturbances.

Anatomical examinations of the two hemispheres of the brain, however, have revealed no structural superiority of one or the other of the cerebral hemispheres. Studies on weight, size, shape, and other characteristics of the hemispheres confirmed the view that they are equal. Inferring function from structure, it is logical to assume that the cerebral hemispheres were equipotential in function. The theory of cerebral dominance assumes that one hemisphere is subordinate, whereas the theory of hemispheric equipotentiality assumes that both cerebral hemispheres function equally. No direct experimental evidence has been

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offered for either theory, yet each is proposed without reference to the other.

REVIEW OF LITERATURE

Evidence for the theory of cerebral dominance in man

1. *As related to the motor function of handedness.* The fact that most of the motor fibers controlling each hand originate in the opposite side of the brain led many to contend that the hemisphere controlling the preferred hand is the lead or dominant hemisphere. The earlier theories of the structural superiority of one cerebral hemisphere were not supported by the facts in subsequent investigations. This led to the belief that one hemisphere is *functionally* superior, but that the differences can not be recognized in structure (Parsons, 1924).

In an attempt to explain why one cerebral hemisphere is functionally superior for hand preference it has been suggested that there is an unequal supply of blood to the two hemispheres. This has been based on the asymmetrical origin of the right and left carotid arteries. Since the heart is on the left side of the body, it was believed that the aorta is in more direct communication with the left cerebral hemisphere than with the right. Parsons (1924) does not accept this view, yet Jordon (1922) and Travis (1931) uphold the belief. Peterson (1932) refutes the theory on the basis of experimentation with lower animals.

2. *As related to disorders of speech.* Accepting the view that an exhibition of a dominant hand in man indicates a dominant hemisphere for motor functions, theorists extended the doctrine to include the function of speech.

Of the earlier writers, Broca, Bouillaud, Wernicke, and others³ localized speech in various areas of the left cerebral hemisphere (for right-handed persons). Marie, Jackson, and Von Monakow disagreed with the localization of speech functions as postulated by these authors, and stated that speech, reading, and writing are functions of the whole of one hemisphere, usually the left in right-handed persons and *vice versa*. Marie thought of the abnormalities as disorders of the intellect and not sensory as up-

³ Reviewed by Meyer (1905), Head (1926), and Travis (1931).

held by Wernicke (Meyer, 1905). Jackson believed that the defect is a defect in propositional thinking.

The theory of cerebral dominance as related to speech had its true beginning with Hughlings Jackson. In 1868 Jackson pointed out (James Taylor, 1931) that there are various degrees of aphasias, and that aphasia, agraphia, and alexia are defects in symbolic thinking. The higher and more voluntary aspects of speech tend to suffer more than the lower or automotive. He alleged that even writing is affected, not as a separate "faculty," but as a part of the failure to propositionise in words.

Jackson formulated his concepts through studies on epileptics. He cited many cases which have a bearing on the later works of Travis and of Orton.

In one of numerous articles Jackson asserts (Taylor, 1931; p. 19):

In all cases of convulsions beginning unilaterally, it is important to consider carefully the side of the body in which the fits begin. We find that when persistent loss of speech occurs with hemiplegia, the hemiplegia is nearly always of the right side. I have long observed of convulsions that when spasms begin on the right side there is a defect of speech more marked than when it begins on the left.

Henry Head (1926) a student and admirer of Jackson, studied many cases of aphasia following cerebral lesions during the war. After extensive study of a number of clinical cases, Head concluded (p. 478):

1. There are no 'centers' for speaking, reading, writing or other forms of behavior comprised in the normal use of language . . .
2. Disorders of speech and similar high-grade defects of function are produced by injury to a single hemisphere, which in strongly right-handed persons is usually the left. . . .

The most recent advocate of the theory of unilateral hemispheric dominance in relation to speech disorders is Travis. The following statement of his is based on the concept of the physiological gradient as postulated by Child (1924), and the works of Head (1926) and of Orton (1925). He states (1931; p. 33):

I believe the dominant center to furnish an inhibitory directional control over the subjacent centers and in the case of the left over the right circumjacent center as follows: Whenever energy is released in a sense organ, it tends to travel to the center of greatest instability (the dominant center), thereby losing some of its value in terms of amount and immediacy of termination for less dominant centers. . . . Anything that increases dominance increases the inhibitory directional control, while anything that decreases dominance decreases such control.

Travis holds that the left hemisphere in right-handed persons is the dominant or lead gradient. He says (p. 34):

Practically no experimental work has been done to determine how sharply the highest dominant gradient may be delimited. But the vast array of clinical material in the form of diseased and injured nervous systems points strongly in the direction of the left cerebral hemisphere of the strictly right-handed individual and the right cerebral hemisphere of the strictly left-handed individual as containing the lead gradient, the more so in relation to such nice activities as speaking, reading, or writing.

The experimental evidence presented in favor of the theory is indirect and the conclusions equivocal. The evidence has been summarized by Travis (1933) who concludes:

It is conceivable that, as the final common motor pathways out of the brain are approached, the right and the left motor impulses in some way, possibly by the former's accepting the latter's rhythm, coalesce to result in the perfect synarchy which is essential for unified control. It is thought-provoking to view this process as a dynamic act of unification on the parts of the two hemispheres producing a oneness in their outputs. Such an idea may be significant for the problem of cerebral hemispheric dominance.

It is indeed thought-provoking, but hardly evidence for the theory of unilateral hemispheric dominance.

In a study of aphasia Weisenburg (1934; p. 32) also supports the theory of cerebral dominance, for he states:

Analysis of the side where the lesions appear in relation to handedness shows that the dominance indicated by handedness is a criterion of the crucial hemisphere for speech in about 95 per cent of the cases.

3. *As related to reading and other visual perceptive processes.* Hinshelwood (1917) stated that a lesion in the left hemisphere in right-handed people, and the right in left-handed people causes word-blindness. This supports the theory of hemispheric dominance in relation to reading defects. Hinshelwood based his conclusions on one autopsy in which the lesion was found to be in the left angular gyrus.

The most recent theory which has had wide publicity and acceptance especially among clinicians is the theory of "stropho-symbolia." Orton (1925) observed that retarded readers usually reverse letters and words in reading. He also observed that some of them are fluent mirror-writers and fluent mirror-readers. He ascribed this ability—or inability—not to a cortical lesion as Hinshelwood had done, but to a "lack of cerebral dominance." The following is a statement of his theory (1928; p. 1096):

.... The first level serves to give awareness that a visual sensation comes from without and is not a recalled memory of things seen; in psychologic terms, this level furnishes the element of external awareness in sensation. This function, without much question, resides in the area striata or calcarine cortex of the occipital lobes. The second level, that of objective memories, serves as the storehouse for visual impressions of objects which have been seen. This function probably resides in the second type of occipital cortex which surrounds the calcarine or striate area. Up to this point the two hemispheres of the brain apparently work in unison to produce a single conscious impression; i.e., the messages relayed from the eyes to the two sides of the brain are fused so as to give only one impression. This is brought into relief by the fact that neither of these functions is entirely lost as a result of the destruction of either hemisphere; a bilateral lesion is required to suppress the function of either the first or the second visual platforms. At the third or associative level, however, destruction in one hemisphere may result in complete loss of the associative function, resulting in inability to read (acquired wordblindness), while destruction of exactly the same area in the opposite hemisphere will not give rise to any symptoms whatever. That hemisphere in which destruction produces loss of the associative function is called the dominant hemisphere, and may be either the left or the right, according to the side which habitually initiates the motor responses of the individual. In other words, it is obvious that the

visual records of one side only are used in symbolic association and those of the other are elided or inactive in this process.

Structurally, however, there is no such contrast between the two hemispheres. The nondominant associative area is as well developed in size and complexity as is the dominant, and current neurologic belief, (neurobiotaxis) would imply that this silent or inactive area must have been irradiated equally with the active to produce an equal growth. Such an irradiation, moreover, would presumably leave behind it some record in the cells of the nondominant side which one may call an engram. The engram in the nondominant side would be opposite in sign, however, from that of the dominant; i.e., it would form a mirrored or antitropic pattern. Under usual circumstances only one of these reciprocally paired engrams operates in association with the concept in reading, as is shown by the facts of acquired word blindness already cited, and its antitropic or mirrored mate is elided or remains inoperative. If, however, the physiologic habit of complete elision of these engrams of the nondominant hemisphere were not established, their persistence might readily serve to explain the failure to differentiate between p and q and between was and saw, and also to account for facility in mirror reading and mirror writing, and thus to explain those confusions of direction which have been extensively recorded in the literature and which as here described seemed to characterize all the cases of my own series. Since this conception of the disability as a physiologic variant differs so widely from the pathologic moment known to result in acquired word blindness, I have felt that the use of the term congenital word blindness was misleading and have offered the term strephosymbolia—twisted symbols—to demarcate better the series of cases showing this typical symptomatology.

It will be noted that Orton assumes three psychological functions, corresponding to three cortical areas. He places "word-blindness" in the third level, whereas Hinshelwood had placed it roughly in the second level. He assumes (1) mnemonic records of letters or words existent in the brain in both dextral and sinistral orientation; (2) cerebral dominance; (3) a reversal of the visual image in the nondominant hemisphere, which normally is suppressed or elided; and (4) a shift of dominance in reversals in reading. Dominance is assumed as a fact but the evidence for it, and an explanation of it, are not given.

Experimental psychologists have not taken cognizance of the theory, yet many educators, clinical psychologists, and medical practitioners have accepted the theory as a working postulate. A few reactions toward the theory as it concerns reading may be mentioned. Tinker (1933; p. 348) believes that

... one is justified in inferring that both left-eyedness and tendencies to sinistral sequences in the perception of words and letters are due to cerebral dominance.

While discussing the tendency of some children to reverse letters and words, Dearborn states (1933; p. 273):

Orton has also given what appears to be an adequate account of this aspect of the difficulty in terms of brain physiology.

After discussing word-blindness, Leo Mayer states (1933; p. 1154):

The third and final important contribution to this subject was made by Dr. S. T. Orton.

Among those critical thinkers who question the theory is Gates who, after discussing Orton's theory, states (1933; p. 4):

It is an explanation that does not explain . . . it offers a purely imaginary picture of brain structures and relations.

In regard to visual perceptive processes other than reading the following may be mentioned. Bender (1933) studied disturbances in visuomotor Gestalt function in cases with organic brain disease. She inferred the locus of the cortical deterioration from the neurological symptoms, and asserts (p. 537):

In every case but one the symptoms pointed to a lesion in the left hemisphere; the one exception was a right-sided lesion in a left-handed man. . . . Thus, in a general way, we may conclude that the area most probably involved in disturbances of the Visuomotor *Gestalt* function, . . . is that between the temporal, parietal and occipital lobes of the dominant hemisphere.

As in most studies of this nature, handedness was not tested before the lesion, and no autopsies were made.

Franz, alone, has attempted an experimental test of the theory of unilateral cerebral dominance. He remarks (1933; p. 874):

As far as I have been able to determine, the hypothesis is based on two series of facts: the preferential use of the right or the left hand for many activities; and the neuropathological correlates of the aphasias.

After describing a number of experiments which presented learning material to the left half of both eyes or to the right half of both eyes, he concluded (1933; p. 875):

... in visual apprehension and learning there is not that hemispherical dominance that has been supposed. Those who invoke the concept of unilateral cerebral dominance should not extend its application to all cerebral functionings without further experiment. Moreover, the exhibition of a definite handedness does not warrant the broad generalizations that have become current.

4. *As related to intelligence and higher mental processes.* In his studies on aphasia Head (1926) emphasized the view that speech could not be localized and that a disorder of speech following a cerebral lesion in the dominant hemisphere was a disorder in "propositional thinking."

Dandy has performed cerebral operations for brain tumors in humans and has observed the effects of these extirpations on intelligence. In his most recent study (1933) he reported three cases of extirpation of most of the right hemispheres with no apparent decrease in mentality. The operations resulted in left-sided hemiplegias but did not affect intelligence. Dandy, however, made no claims for cerebral dominance, for he did not mention the handedness of the individuals, nor did he have comparable cases with extirpations of the left hemisphere. It is implied by others, however, that the left hemisphere is functional in intelligence. Diven (1934) interprets these results as indicating that mental activity is localized in the left hemisphere for right-handed individuals.

5. *Summary.* The theory of cerebral dominance in man has

been applied to (1) the motor function of handedness; (2) the function of speech; (3) the visual perceptive functions of reading and other processes not involving language; and (4) intelligence and higher mental processes. In clinical practice a test of the dominant hand is accepted as a test of the dominant hemisphere. Lesions in the contralateral hemisphere supposedly result in disturbances of any or all of these functions, whereas lesions in the homolateral hemisphere do not disturb these functions.

Experimental pathological studies on animals

Studies of psychological disorders following controlled cerebral lesions in animals have shown certain functions to be similar to those found in man. In the rat are found (1) the motor function of handedness, (2) the ability to discriminate visual patterns, and (3) the ability to relate isolated experiences without learning (intelligent behavior). The more important studies relating to our investigation on the rat are summarized below:

1. *Studies on handedness in the rat.* Yoshioka (1930), Tsai and Maurer (1930), and Peterson (1931) discovered that rats exhibit a definite hand preference. This function was tested by a feeding situation in which the rat was required to reach for food with one or the other of its hands. It was found in several experiments that the handedness of the rat was a consistent and permanent characteristic. Peterson's experiment (1934) showed that the feeding situation was a reliable test of handedness in the rat. The consistency could not be explained by chance or habit.

Peterson (1931, 1934) has further shown that the hand preference of the rat in the feeding situation is dependent upon intact motor and somaesthetic fields of the opposite cerebral hemisphere. Lesions within a localized area in the frontal region of the contralateral hemisphere led to a transfer in the preferential use of the hands, whereas similar lesions in the homolateral hemisphere did not influence handedness.

2. *The visual function.* Lashley, in extensive studies on brightness discrimination and on pattern vision in the rat, assumed hemispheric equipotentiality although he did not deal directly

with the theory. Lashley was interested in studying the effects of symmetrically bilateral lesions on the retention of the habit of brightness discrimination and of pattern vision.

In his earlier studies on brightness discrimination Lashley (1926, 1929) stated that: (1) Bilateral destruction of the whole of the posterior third of the cortex, after the brightness discrimination habit had been established, resulted in a loss of the habit. The loss, as measured by relearning, "was closely proportional to the extent of the injury and independent of its locus within the occipital third of the cortex." (2) Cerebral lesions in the frontal and parietal areas of the cortex did not affect the formation of the brightness habit, nor did they affect the performance of the acquired habit. In his most recent study (1935) he retracted some of the earlier conclusions and asserted that the retention of brightness discrimination was dependent upon intact striate areas, although relearning was not influenced.

Studies of the effects of cortical destruction on the acquisition or retention of reaction to a visual pattern for the rat are of recent date, and have been performed mostly by Lashley. The development of his jumping apparatus (1930) was the starting point for these studies. Previous to the advent of this apparatus, discrimination of form and size was not adequately demonstrated in the rat. With this apparatus it was found that rats could readily learn to respond to complex visual forms. This led to studies of cerebral functioning in relation to the acquisition and retention of response to visual patterns.

Lashley's earlier studies (1931, 1932) indicated that the rats failed to acquire the habit of reaction to a visual pattern when the optic radiations were interrupted. Postoperative disturbances, however, did not follow lesions in other than the posterior third of the cortex. In a later study of bilateral cortical destruction in relation to the retention of pattern vision, Lashley (1934) felt justified in drawing the conclusions: (1) complete destruction of both striate areas permanently abolishes pattern vision; (2) the postoperative disturbance was not dependent upon the extent of cortical tissue destroyed outside of the striate area. It appears that vision is more or less localized in the striate area, although

the evidence is not conclusive or applicable to all complexities of visual patterns. It is safe to say that detail vision is localized in the posterior cortex and probably specifically in the striate area. The localization is not as specific as that for the function of handedness, but could not be considered general.

3. *The function of intelligence.* Studies dealing with the intelligent functions in the rat have almost exclusively dealt with bilateral lesions. Lashley (1929) studied the effects of bilateral cortical lesions on the capacity to form maze habits and on the retention of these habits. He concluded that the capacity to learn and the capacity to retain is reduced in proportion to the extent of cortical injury and not upon its anatomical specialization in the cortex. Thus, for the maze habit, lesions in any portion of the cortex result in a similar decrease in capacity. This makes the maze habit a general function and not dependent specifically on one cortical area (as the motor area) or upon a less specific function (as that of the visual area).

Maier (1929) has demonstrated that rats can combine the essentials of two isolated experiences in such a way as to reach a goal, when the experiences were not contiguous in time or space. In his experiments he set up a number of problems which furnished (1) an exploratory experience, (2) a feeding experience, and (3) the relating of these two isolated experiences in order to reach the goal. He states (1931) that this behavior cannot be explained by the traditional laws of association (contiguity, recency, frequency, intensity, primacy, etc.) and has designated this ability as "reasoning."

In later experiments (1932) he has presented evidence showing that reasoning (as defined above) and learning are qualitatively different. Experiments on the function of the cerebrum in relation to reasoning indicated that the ability is decreased in proportion to the extent of the lesion, regardless of its locus.

The experiments on the effect of cerebral destructions on reasoning have dealt wholly with more or less symmetrically bilateral lesions. No effects of unilateral lesions have been studied. Again hemispheric equipotentiality was assumed.

Summary of literature

Among the psychological functions ascribed to the dominant hemisphere in man are found (1) the motor function of handedness, (2) the visual-perceptive functions and (3) the functions of intelligence. These three processes have also been demonstrated in the rat. Experimental-pathological studies have tacitly assumed that the rats' hemispheres are equipotential, and disturbances of the functions (with the exception of handedness) have been studied by means of controlled bilateral lesions. These studies have shown (1) that handedness is more or less specifically localized in the motor area; (2) that visuo-motor habits are less specific in localization but may be ascribed to the posterior third of the cortex or specifically to the striate area; and (3) that intelligence (learning and reasoning) are very general and not at all localized. Since the rat exhibits a definite hand preference, it is now possible to study whether or not, the exhibition of a dominant hand is an indication of a dominant hemisphere for other psychological processes as well.

THE PROBLEM AND METHODS OF EXPERIMENTATION

The present problem

The purpose of this investigation is to furnish experimental evidence in the case of the rat for one or the other of the opposing assumptions, hemispheric cerebral dominance and hemispheric equipotentiality. By studying the effects of unilateral cortical lesions on (1) handedness, (2) retention of reaction to a visual pattern, and (3) intelligent behavior, the factor of dominance can be tested in specific, partially specific, and general functions, respectively.

General method of experimentation

With apparatus to be described later, the rats were (1) tested for hand preference, (2) trained to give a selective response to a visual pattern, and (3) tested for intelligent behavior on Maier's reasoning test. When the tests and training were completed, the animals were subjected to cerebral insults. For one group

of animals the lesions were on the hemisphere opposite to the preferred hand (contralateral hemisphere); and for the other group the lesions were on the hemisphere of the same side as the preferred hand (homolateral hemisphere).

After a ten day period allowed for recovery from the operations, the rats were given postoperative tests of handedness, of retention of the visual patterns, and of reasoning ability. Histological studies of the brains were made at the completion of the postoperative tests.

Subjects

Forty-eight adult albino rats were used in the experiments. Of the 48 animals, 6 did not survive the operations and 1 died before completion of the tests. Thus there are records on handedness for 41 rats. A number of animals would not jump to the visual forms and were therefore excluded from the pattern-vision experiment. Only 28 rats completed the pre- and postoperative tests for this aspect of the investigation. For reasoning or intelligent behavior there are data on 37 rats since 1 rat would not run and 3 died before the experiment was completed. Rats number 10, 14, and 40 were males while the others were all females.

Surgical and histological methods

Each animal was trephined in one or two places on only one side, and cortex was destroyed by means of thermocautery. When the postoperative tests were completed the animals were killed and the brains were removed. The brains were then fixed, and the lesions were reconstructed on brain charts according to the method described by Lashley (1929).

The tests used

1. *The handedness test.* A T-shaped metal feeding cup similar to a canary feeding dish (Peterson, 1931) was constructed for the handedness test. The base of the T, which was narrow so that the rat could not reach the food with his mouth or tongue, was inserted between the wires of the cage. In order to feed, the rat was forced to reach the food (oatmeal) with one of his paws.

The tests were given in a rectangular wire cage divided by a board into two corresponding cages with a feeding cup in each.

Very few of the rats spontaneously used their hands on the first day. They scratched at the cage, projected their tongues into the feeding cup, or finally left the cup entirely. Several rats were placed in the cages for eleven days before they began using their paws. After the first successful attempt, however, the rats usually went directly to the feeding cup and used one of their hands to bring up the food. In order to avoid a place association with the surroundings of the cage, the rat was tested sometimes in one cage and sometimes in the other. Each rat was tested over a period of four days, and the successful reaches for food with each hand were counted until a total of 75 trials had been recorded. The test was given before and after the operation.

2. *The pattern vision test.* A jumping apparatus similar to that described by Lashley (1930) was used to secure responses to the visual patterns. The apparatus was built according to specifications except that the stand from which the rats jumped was a 6-inch circular disc mounted on a ring stand and attached to a window sill. As in Lashley's experiment the rats jumped away from the light.

In training the animals, the stand was first placed near the screen and the rats were allowed to step through the openings to the platform in order to obtain food. The distance between the screen and the stand was gradually increased until the rats were jumping through the windows from a distance of 25 cm. Then two white cards, held in place by light springs, were placed in the two openings. As the rats jumped at either window, the card fell back easily on the feeding shelf. Some rats showed no hesitancy in jumping at the white cards, while others refused to jump. In the latter cases, the stand was brought close enough for the rats to push down the white card by stretching, and then step through the open window. Again the distance was gradually increased until the rats were jumping at the white cards from a distance of 25 cm. When a rat had learned to jump freely with two white cards exposed, one of the white cards was changed for a black one held firmly in place so that the animal could not get

through that window. This was changed irregularly from one window to the other until the rat learned to give a positive response to the white card, regardless of its position. The time required for this procedure varied from one to twenty days for the different rats.

After an animal had learned to jump to a white card alternated irregularly with a black one, the following visual patterns were presented (figure 1). The rats were trained to respond positively to the normal F and negatively to the mirrored F.

At this point it was very common for the rats to establish a place association and to jump consistently either to the right or to the left window. If the rat jumped to the same window for all ten trials of one day, the place association was broken the



FIG. 1. THE VISUAL PATTERNS USED IN THE PRESENT EXPERIMENT
The figures are reduced to one-sixth the original size

next day by again presenting the animal with white and black cards—the black card being placed in the window toward which he had been jumping consistently, and the white card in the other window. Usually three to five trials of this were sufficient to break the place association. If not, the procedure was continued until the habit had been broken.

Although some rats jumped readily as soon as they were placed on the stand, a few rats required urging by hitting or jarring the stand. The rats usually jumped more readily after learning had once begun. On the postoperative trials, the rats were much slower in jumping and required more urging. A few rats jumped for several hundred trials and then suddenly refused to jump. There seemed to be very little correlation between speed of response and rapidity of learning, for some rats needed urging yet

learned rather rapidly; while other rats jumped very quickly, but required many more trials to learn.

Conditions of preoperative and postoperative learning. The rats were given 10 trials every day in jumping to the visual patterns. The position of the figures was changed irregularly. The training was continued until the rats had learned to a criterion of 50 errorless trials over a period of five consecutive days.

After a ten-day rest, the animals were given a *preoperative retention test* which covered a period of five days. On the first two days 10 trials each were given as before, except that both windows were unlatched in order to test the rat's preference without the influence of relearning. On the last three days relearning was tested by repeating the conditions of the original learning. After this the operations were performed.

Following the ten days which were allowed for recovery from the operations the rats were given *postoperative tests*. These were the same as the preoperative tests except that relearning continued until one of the following two criteria was reached: (1) 30 errorless trials in three consecutive days (100 per cent success); or (2) 25 correct jumps out of 30 trials in three consecutive days (83 per cent success). The second criterion was used since two of the animals did not reach the first criterion of 100 per cent success. (Rat number 40 died after 280 trials; rat number 22 was discontinued after 330 trials.) Consequently we have 26 rats for the first and 28 for the second criterion.

3. *Test of intelligent behavior—"reasoning."* As previously described by Maier (1932, 1932a) the apparatus for this test consisted of three tables connected by elevated runways $1\frac{1}{2}$ inches in width. The tables were of differing shapes, and were screened from the runways by large cardboards with holes large enough for the rats to pass through.

In the preliminary period the rats were allowed to explore the tables daily for one hour. At the end of the exploratory period of two weeks they were fed on any one of the tables. In the actual test situation the rats were again allowed to explore the tables for ten or fifteen minutes—experience 1. They were then carried to one of the tables where they were given a small amount

of food. The experience of food on a specific table may be considered experience 2. The test consisted of placing the rat on one of the other two tables and observing whether it would proceed directly to the table on which it had experienced food. This test was repeated for eighteen days using different combinations of tables. In order to make better than a chance score the animal was required to relate experience 1 with experience 2, both of which had been presented in isolation. The rats were tested six days a week for three weeks (eighteen days) before operation, and similarly after operation.

RESULTS

A. The effect of contralateral cortical lesions on handedness

The validity of the handedness test. Peterson (1934) has contended that the feeding situation is an adequate test of a rat's hand preference. Our handedness data were also analyzed for the purpose of determining whether or not the rat's hand preference was the result of habit, or factors inherent in the test situation. For 24 of the rats a record was kept of the hand used and of the bodily position taken in relation to the feeding cup for two test periods of 75 trials (four days) each. This was done for (1) the original preoperative test, and (2) a second preoperative test six weeks later.

That the preference is not a matter of chance or habit is suggested from the following three lines of evidence:⁴

1. Some rats began with one hand but soon changed and used the other hand consistently after the first few reaches. Even in those cases which were consistent from the very first reach, the habit was probably not formed by so few trials, for other habits are not so readily established in the rat.

2. The position the rat took in relation to the feeding cup did not seem to determine the hand he used consistently, but rather, the hand preferred seemed to determine the position taken. The

⁴ Complete data is presented in the author's dissertation "The Effects of Unilateral Cortical Lesions on Handedness, Pattern Vision, and Reasoning in the Albino Rat," filed in the University of Michigan Library.

side of the cup opposite to the preferred hand apparently afforded much more efficient feeding. Of the animals whose handedness was changed after the operation none made a radical shift in position, but thereafter tended to feed from an inconvenient position. The position habit appeared to have been readily established because of the original hand preference.

TABLE 1
Showing consistency of handedness test

NUMBER OF RAT	FIRST TEST	SECOND TEST SIX WEEKS LATER
1	70 L— 5 R	74 L— 1 R
2	75 R— 0 L	75 R— 0 L
3	75 R— 0 L	64 R—11 L
4	75 R— 0 L	75 R— 0 L
5	75 R— 0 L	75 R— 0 L
6	75 R— 0 L	75 R— 0 L
7	45 L—30 R	66 L— 9 R
8	72 L— 3 R	73 L— 2 R
9	75 L— 0 R	75 L— 0 R
12	75 R— 0 L	75 R— 0 L
13	75 L— 0 R	75 L— 0 R
15	75 L— 0 R	75 L— 0 R
25	74 L— 1 R	75 L— 0 R
26	75 L— 0 R	75 L— 0 R
27	75 L— 0 R	75 L— 0 R
28	71 L— 4 R	75 L— 0 R
32	75 L— 0 R	70 L— 5 R
34	75 R— 0 L	75 R— 0 L
35	63 L—12 R	71 L— 4 R
37	75 L— 0 R	75 L— 0 R
38	75 R— 0 L	43 R—32 L
39	75 R— 0 L	75 R— 0 L
42	74 L— 1 R	75 L— 0 R
43	46 L—29 R	75 L— 0 R

3. The test was a reliable indication of the rats handedness. The results of the two preoperative tests are presented in table 1. It will be noted that for all rats the results are quite consistent. The most marked differences are found with rats numbers 38 and 43. Rat number 43, who was ambidextrous with a slight sinistral tendency on the first test, became purely left-handed on the second test. Rat number 38, who was purely right-handed

on the first test, became ambidextrous with a dextral tendency on the second test. Still less significant differences are found in the results on rats numbers 3 and 7, who, however, retained their ambidextrous classification. *In no case did a rat change from a predominantly left- to a predominantly right-handed tendency, or vice versa.* In other words, the handedness classification (right or left) as determined by the majority of reaches in 75 trials did not change for any rat. It was therefore unnecessary to test handedness over a longer period or with more trials. On the contrary, it was desirable to determine handedness with the least amount of practice in order to exclude any possible influence of practice.

The foregoing arguments and evidence tend strongly to suggest that for the rat testing hand preference by the feeding situation over a short period of time is adequate to determine handedness. The handedness of the rat as determined by the feeding situation appears, therefore, to be a stable and permanent characteristic.

Results of cerebral destructions. For all rats the post-operative handedness tests were begun ten days after the operation. The method of testing was the same as in the preoperative tests.

Table 2 presents the pre- and postoperative trials for handedness of 21 rats with contralateral lesions and 20 rats with homolateral lesions. Of the 21 animals with contralateral lesions, 1 rat (number 18) showed a partial change of handedness; 10 showed a complete change; while 10 showed no change. It should be noted that rat number 3 is not considered as having changed handedness. In the first place, as is shown in table 1, rat number 3 showed some ambidextrous tendency on the second preoperative test. Although on the first preoperative test it reached 75 times with its right hand, on the second preoperative test it reached 64 times with its right hand and 11 times with its left hand, indicating partial ambidexterity before the operation. Rat number 18 was considered to have shown a partial change of handedness. This case will be explained later.

The critical area necessary for handedness. An explanation of why some rats with contralateral lesions changed handedness while others did not is furnished in figure 2. It should be noted

TABLE 2

The effect of contralateral and homolateral cerebral lesions on handedness

NUMBER OF RAT	PERCENTAGE OF LESION	PREOPERATIVE HANDEDNESS	POSTOPERATIVE HANDEDNESS
Contralateral lesions			
Partial change of handedness			
18	15.9	L-75	L-40 R-35
Complete change of handedness			
23	21.3	L-75	R-75
24	21.5	R-67 L- 8	L-75
25	21.7	L-74 R- 1	R-75
28	23.0	L-71 R- 4	R-75
29	23.0	R-75	L-75
32	25.0	L-75	R-75
35	25.1	L-63 R-12	R-75
38	25.9	R-75	L-75
40	27.5	R-75	L-75
41	29.2	R-75	L-75
No change of handedness			
3	7.6	R-75	R-59 L-16
4	7.8	R-75	R-75
5	7.8	R-75	R-75
7	9.6	L-45 R-30	L-75
9	10.8	L-75	L-75
10	12.1	R-73 L- 2	R-75
12	12.3	R-75	R-75
13	13.2	L-75	L-75
16	14.7	R-75	R-75
20	17.0	R-75	R-75
Homolateral lesions—(no changes)			
1	5.5	L-70 R- 5	L-75
2	6.4	R-75	R-75
6	8.6	R-75	R-74 L- 1
8	10.5	L-72 R- 3	L-71 R- 4
11	12.3	L-75	L-75
14	13.5	R-75	R-75
15	13.8	L-75	L-55 died
17	14.9	R-75	R-75
19	16.3	L-75	L-75
21	17.8	R-75	R-75
22	18.7	R-75	R-75
26	21.9	L-75	L-75
27	22.8	L-75	L-75
30	23.3	R-75	R-75
31	23.6	L-75	L-75
33	25.0	L-75	L-75
34	25.1	R-75	R-75
36	25.4	L-75	L-75
37	25.6	L-75	L-75
39	26.5	R-75	R-75

that all lesions included a part of the posterior portion of the cortex. While some rats received lesions only in this region, others received lesions extending from the posterior to the anterior sections of the hemisphere.

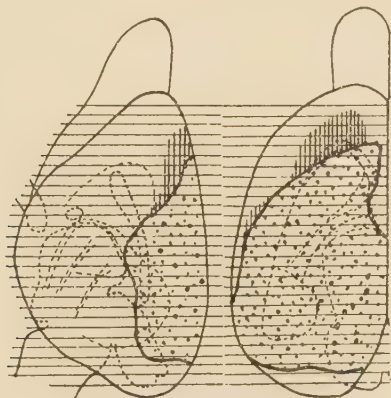


FIG. 2. The *stippled portion* represents a composite area of the cerebral destructions of those 10 rats with contralateral lesions who showed no change in handedness. The *hatched portion* represents the remaining common area for the 10 rats who showed complete changes of handedness. In this figure the composite of the 10 rats that did not change handedness is subtracted from the common area of those rats that changed handedness; thus leaving the *hatched portion*; an area which, when extirpated, always resulted in a complete change of handedness.

The stippled portion in figure 2 represents the combined area of the cerebral destructions of those 10 rats with contralateral lesions who showed no change of handedness. The hatched portion represents the remaining common area for the 10 rats who showed complete changes of handedness. In this figure the composite of the 10 rats that did not change handedness is subtracted from the common area of those rats that changed handedness; thus leaving the hatched portion, or the critical area, which, when extirpated, always resulted in a complete change of handedness. It should be pointed out that these areas are only approximations, but indicate that there is some localization for the use of the preferred hand.

The reader will note that rat number 18 had been eliminated from the previous considerations. This rat changed from a left-hand preference to ambidexterity after a contralateral lesion.

For this reason he could not be included in the group who showed complete change of handedness, nor in the group who showed no change of handedness. In figure 3 is shown the extent to which this animal's lesion overlaps the common area for the ten rats who showed complete changes of handedness. It appears that this one rat, whose lesion included approximately one-half of the "critical" area, showed an incomplete shift of handedness.

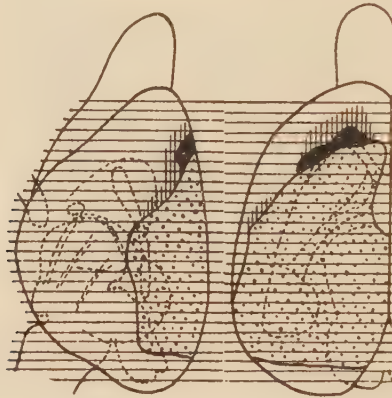


FIG. 3. The black portion represents the extent to which the lesion of rat 18 overlaps the common area of the 10 rats who showed complete changes in handedness (cf., fig. 2).

Unfortunately we have only one rat falling in this classification and therefore no conclusions can be made. Two explanations, however, seem plausible: (1) rat number 18 might have become ambidextrous without the operation as in the case of rat number 38 (table 1); and (2) extirpation of a portion of the critical area necessary for handedness might result in a partial shift of handedness; i.e., mass action within the critical area.

It is interesting to note the correspondence between the locus of Lashley's (1921) electrically stimulable points for arm and hand movement, and our critical area for handedness as shown in figure 4. The stimulable points, *k* (elbow flexed), *j* (forearm retracted), *i* (shoulder drawn forward), *l* (elbow extended), and *m* (wrist flexed) fall within or adjacent to our critical area for handedness. This correspondence leads to the conclusion that the critical area for handedness is approximately the same as the

stimulable cortical points resulting in contralateral arm and hand movements.

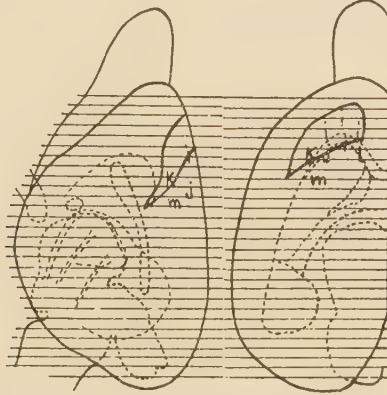


FIG. 4. THE CORRESPONDENCE OF THE CRITICAL AREA NECESSARY FOR CHANGE OF HANDEDNESS IN THE RAT, AND THE ELECTRICALLY STIMULABLE POINTS FOR ARM AND HAND MOVEMENT

The stimulable cortical points (after Lashley 1921) falling in or adjacent to the critical area are: *k*, elbow flexed; *j*, forearm retracted; *i*, shoulder drawn forward; *l*, elbow extended; and *m*, wrist flexed.

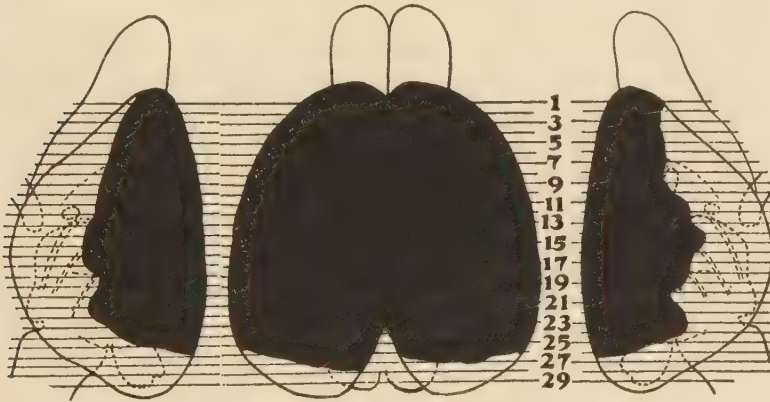


FIG. 5. SHOWING THE EXTENT AND LOCUS OF THE COMPOSITE AREAS OF THE HOMOLATERAL AND CONTRALATERAL LESIONS

The left half of the figure represents the composite area of the 21 rats receiving contralateral lesions; the right half represents the composite of the 20 rats with homolateral lesions. The average lesion for the contralateral group was 17.7 per cent; and for the homolateral lesions, 17.9 per cent.

Of the 20 rats with homolateral lesions, none showed a change of handedness. Figure 5 shows the similarity between the com-

posite lesions in the homolateral and contralateral hemispheres. The average percentages of lesion for the two groups are approximately identical—17.7 per cent for the contralateral lesions and 17.9 per cent for the homolateral lesions.

Peterson (1934) has shown that after cerebral destructions in the critical area the rat changes its hand preference. Furthermore, he found that these changes resulted even when subcortical tissue was not invaded. In the present experiment the corpus collosum, the caudate nucleus, and the hippocampus were invaded in every rat that changed handedness. These were also invaded to a similar degree in many of the rats that did not change handedness.

Discussion

It seems apparent that the mechanism of handedness in the rat is dependent upon a definitely localized area in the contralateral hemisphere, and is not general as assumed by the theory of cerebral dominance. There still remains the possibility of mass action within the critical area as is suggested by the results on rat number 18.

Peterson (1934) has shown that the hand used after operation is used only from preference. Disabling the newly preferred hand with adhesive tape after a contralateral operation resulted in the use of the originally preferred hand only during the period of disability, but did not interfere with the postoperative preference after the tape was removed. He states (p. 16):

The brain may be regarded as a necessary part of a mechanism which reveals handedness. Removing any part of the mechanism necessarily interferes with its functions, as would be obviously true if the hand itself were removed.

The present writer cannot completely agree with this statement on the basis of Peterson's own data. Removal of a hand permanently disables that hand. Removal of the cortex changes only the hand *preference*, not the *ability to use* that hand. Re-education of the non-preferred hand over an extensive period of time may throw further light on the mechanism of handedness in the rat.

No adequate explanation can be given to account for hand preference in the rat. The fact that a localized cortical lesion changes this preference indicates that a critical area in one hemisphere is functional for this behavior pattern. It does not explain "dominance."

Conclusions for handedness

An analysis of the anatomical and behavioral data in terms of handedness leads to the following conclusions:

1. When a cortical lesion invaded a critical area of the motor and somaesthetic fields of the contralateral hemisphere, our rats changed handedness in the feeding situation.
2. When a lesion fell posterior to the critical area in the contralateral hemisphere, no change of handedness resulted.
3. Regardless of the extent or locus of the cortical destructions in the homolateral hemisphere within the limits of our lesions no change of handedness resulted for any rat.
4. The critical area for handedness corresponds approximately with the electrically stimuable cortical points for arm and hand movements.

B. The effect of contralateral cortical lesions on pattern vision

In so far as hemispheric dominance is based on a demonstration of a definitely preferred hand, it follows that the rat also has a "dominant" and a "non-dominant" hemisphere, since it exhibits distinct hand preference. In the foregoing sections evidence has been presented to show that for hand preference a certain critical area of the cortex is dominant over a corresponding area in the opposite hemisphere; and that removal of this critical area changes the dominance to the opposite hemisphere (as measured by hand preference). The present problem deals mainly with determining whether such a dominance is related to the perceptual function of pattern vision in the rat. In this connection we may raise several problems.

The first problem is concerned with the question of *whether there is a dominant hemisphere which controls learning, and which, when injured cortically, results in the loss of an acquired ability to*

respond to a visual pattern. Table 3 presents the data on sixteen rats with contralateral lesions and twelve rats⁵ with homolateral lesions. The numbers of the rats (column 1) and the percentages of lesions (column 2) correspond to the numbers and percentages of lesions given on the brain charts in the appendix. Columns 3 and 4 show respectively the number of trials and number of errors required for initial learning to the criterion of fifty consecutive errorless trials. Columns 5 and 6 refer similarly to trials and errors required for postoperative relearning (trials and errors preceding 30 errorless trials in three consecutive days). Column 7 shows postoperative errors to and *including* the 25 errorless jumps out of the 30 trials in three consecutive days (83 per cent criterion). Trials were eliminated here since by this criterion there was no differentiation between animals making no errors and those making up to five errors within the minimum 30 trials.

According to the theory of unilateral cerebral dominance, the group of rats with contralateral lesions should lose the habit of responding correctly to the visual patterns; whereas the group with homolateral lesions should tend to retain the ability. The data presented in table 3 do not uphold the theory, but rather indicate that the hemispheres are equipotential for pattern vision. This is shown from two differing modes of analyzing the data.

1. In considering the number of cases of each group which retained the habit, we shall arbitrarily consider 6 or less errors on

⁵ Of the 41 rats used for the handedness experiment, 13 did not complete the tests for pattern vision. These are: (1) Rats numbers 17, 26, 32, 38, and 39, who, on the preoperative tests, could not be trained to jump, or who refused to continue jumping after bumping their noses several times. (2) Rats numbers 33, 34, and 35, who, in 600 preoperative trials could not learn to the criterion of 50 errorless trials. (3) Rats numbers 31, 36, and 41, who refused to jump after the operations. These rats were also very poor jumpers before the operations. Rats numbers 31 and 36 received homolateral lesions; rat number 41, contralateral. (4) Rat number 15, who died before completion of the postoperative retention test. (5) Rat number 23, who did not complete postoperative relearning. Even in initial training, this animal had difficulty in jumping directly at the windows. After the operation this peculiarity was so exaggerated that he could not relearn in 500 trials. With the results on these animals eliminated, we have 26 rats who relearned to 100 per cent perfection or 28 rats who relearned to at least 83 per cent perfection.

TABLE 3

The effect of contralateral and homolateral cerebral lesions on the retention of pattern vision

NUMBER OF RAT	PERCENTAGE OF LESION	INITIAL LEARNING		POSTOPERATIVE RETENTION		
				100 per cent criterion		83 per cent criterion
		Trials	Errors	Trials	Errors	Errors
Contralateral lesions						
3	7.6	200	63	0	0	0
4	7.8	365	123	20	5	5
5	7.8	299	80	20	9	9
7	9.6	149	29	16	3	3
9	10.8	235	58	52	16	16
10	12.1	104	42	18	3	3
12	12.3	190	58	61	21	21
13	13.2	230	72	25	5	5
16	14.7	122	49	0	0	0
18	15.9	160	77	277	120	120
20	17.0	76	29	120	51	51
24	21.5	189	47	128	47	39
25	21.7	133	44	89	33	30
28	23.0	125	51	159	35	10
29	23.0	146	29	97	36	36
40	27.5	197	79	*	*	52
Average.....	15.3	183	58.1	72	25.6	25
Homolateral lesions						
1	5.5	387	131	11	3	3
2	6.4	167	65	100	24	5
6	8.6	339	101	45	9	7
8	10.5	140	44	134	47	43
11	12.3	156	51	140	62	62
14	13.5	108	48	30	5	5
19	16.3	109	51	20	5	5
21	17.8	161	59	274	77	46
22	18.7	278	66	*	*	75
27	22.8	109	42	240	74	61
30	23.3	76	29	20	4	4
37	25.6	120	43	119	52	52
Average.....	15.1	179	60.8	103	32.9	30.6

* Did not learn to the criterion of 30 errorless trials (100 per cent).

the postoperative tests as indicating immediate retention since this was the highest error obtained on the pre-operative retention tests. Using the 100 per cent criterion, we note that 4 of the 11 rats of the homolateral group (36 per cent) retained the ability, while 6 of the 15 rats of the contralateral group (40 per cent) also retained the ability. Similarly, using the 83 per cent criterion, 5 of the 12 animals of the homolateral group (42 per cent) and 6 of the 16 animals of the contralateral group (37 per cent) retained the ability. It is also obvious that when we consider loss of the habit, there is a comparable number from each group which made more than 6 errors. By these measures, it may be concluded that the hemispheres are equipotential; i.e., cortical lesions produce similar disturbances of the habit of reaction to a visual pattern whether the lesion is in the homolateral or in the contralateral hemisphere.

2. Considering the average scores for the two groups, we find that there are but slight differences between these two in percentages of lesion and in initial learning scores. It should also be noted that the locus of lesions for both groups is very similar, as may be readily seen from the brain charts in the appendix. According to the theory of cerebral dominance there should be greater retention by the group with lesions in the homolateral hemisphere, but our results show, if anything, a slight trend in the opposite direction. The average postoperative retention scores for the contralateral group were: 72 trials and 25.6 errors for the 100 per cent criterion; and 25.0 errors for the 83 per cent criterion. For the homolateral group the corresponding scores were: 103 trials and 32.9 errors for the 100 per cent criterion; and 30.6 errors for the 83 per cent criterion. These scores indicate that the group with lesions in the homolateral hemisphere took more trials and made more errors than did the group with lesions in the contralateral hemisphere. This difference, of course, is probably due to chance factors and might be expected from the averages of small groups.

Thus by neither method of analysis do we find a greater loss from the contralateral lesions. Instead, the evidence points to hemispheric equipotentiality.

The second problem is related to the theory of "strephosymbolia." In this connection one may ask: *Is there any indication that after a posterior lesion in the contralateral hemisphere the animal will jump toward the reversed figure?*

Orton (1925) has postulated that when there is a conflict in cerebral dominance of a human the person tends to reverse words and letters in reading them. According to Orton, these symbols are "etched" normally in the contralateral and mirrored in the homolateral hemispheres in the third (visual associative) level. In the condition of lack of cerebral dominance the mirrored symbol in the homolateral hemisphere causes a reversed response.

According to this theory a child learning the word "no," for example, will have an engram of "no" in the contralateral hemisphere, and an engram of mirrored "no" in the homolateral hemisphere. In normal reading the contralateral hemisphere is functional, while the engram of mirrored "no" in the homolateral hemisphere is elided. In the event of a lesion or a decrease in the dominance of the contralateral hemisphere, there results a verbal motor response, "on," to the visual symbol "no."

In our experimental situation the rats were trained to give a positive motor reaction (jump) to the pattern F, and a negative motor reaction to its mirrored counterpart (mirrored F). If Orton's theory were applicable to the rodent, we should expect that a lesion in the contralateral hemisphere should decrease the dominance of that hemisphere and result in the functioning of the previously non-dominant hemisphere (the homolateral hemisphere). In this case we should expect the rat to respond positively to the mirrored F and negatively to the normal F. The criticism may be raised that we have no evidence for the third visual level (visual associative) in the rat, but such a criticism is readily answered by the fact that neither has the level been demonstrated for humans.

Table 4 presents the data on the effects of contralateral and homolateral lesions in producing a tendency to respond to reversed figures. In column 3 are presented the preoperative retention scores for the first two days of the test. The scores are given in terms of right minus wrong responses. The cards pre-

TABLE 4

The effect of contralateral and homolateral cerebral lesions on reversals

NUMBER OF RAT	PERCENTAGE OF LESION	PREOPERATIVE RETENTION TEST (R-W)	POSTOPERATIVE RETENTION TEST (R-W)
Contralateral lesions			
3	7.6	18	18
4	7.8	8	0
5	7.8	18	2
7	9.6	20	8
9	10.8	20	6
10	12.1	18	2
12	12.3	20	4
13	13.2	4	10
16	14.7	20	14
18	15.9	18	0
20	17.0	0	0
24	21.5	16	0
25	21.7	16	0
28	23.0	0	4
29	23.0	20	0
40	27.5	18	2
Average.....	15.3	14.6	4.4
Homolateral lesions			
1	5.5	2	2
2	6.4	16	8
6	8.6	20	0
8	10.5	8	0
11	12.3	12	0
14	13.5	20	0
19	16.3	20	14
21	17.8	20	0
22	18.7	12	0
27	22.8	16	-6
30	23.3	20	4
37	25.6	20	0
Average.....	15.1	15.5	1.8

sented were both unlatched so that no relearning could take place. In column 4 are given the postoperative retention scores for the same conditions after the operations.

The average percentage of lesion and the preoperative retention scores are approximately the same for the two groups. According to the theory we should expect minus scores from animals with contralateral lesions. This would be the case if the rats responded positively to the reversed pattern (mirrored F). The results did not show this to be so, for only one negative score occurred, and that was in the homolateral group. This is what would be expected on the basis of the preceding section which showed that the hemispheres of the rat are equipotential for pattern vision, whereas the theory of "strephosymbolia" is based on the assumption of hemispheric dominance.

We make no claims of analogy from rat to man. Our results are only applicable to the rat. Furthermore, it must be pointed out that this is not a conclusive test of Orton's theory. It is believed, however, that the theory of "strephosymbolia" is highly speculative, and before it can be accepted its existence should be supported by some evidence other than that derived from numerous assumptions (see p. 6).

A third problem raised is concerned with the *relation between the extent of cortical destruction and the degree of postoperative disturbance*.

An explanation for the disturbance of the habit of reaction to the visual pattern is found in the relation between extent of cortical lesion and degree of postoperative disturbance. Kirk has analyzed these data elsewhere. A correlation of extent of lesion with postoperative trials was $+0.48$ and with postoperative errors $+0.52$. An analysis of the data showed that the disturbance of the habit was not dependent upon (1) the extent of striate area destroyed; (2) the locus of striate area destroyed; or (3) the extent of posterior lesion. From these results it was concluded that:

1. The loss of the habit of reaction to a complex visual pattern in terms of relearning is closely proportional to the extent of the lesion and is not mainly dependent upon the destruction in the area striata or the posterior cortex.

2. The results may be interpreted as evidence for extra-striate functions in the discrimination of complex visual patterns.

Conclusions for Pattern Vision

1. Retention of a motor response to a visual pattern suffers the same loss from a homolateral lesion as from a contralateral lesion. There is no evidence for hemispheric cerebral dominance in the rat; rather, the hemispheres appear to be equipotential for this function.

2. A cerebral destruction in the contralateral hemisphere does not produce a positive response to a pattern which is the reverse of the one to which the response had been previously established.

3. In terms of relearning the loss of the habit of reaction to a difficult visual pattern is closely proportional to the extent of the lesion and is not entirely dependent upon the destruction in the area striata.

C. The effect of contralateral cortical lesions on intelligent behavior

Table 5 gives the pre- and postoperative scores on Maier's reasoning test for two groups of rats—a group with homolateral lesions and a group with contralateral lesions. Columns 3 and 4 present the preoperative scores in terms of the number of correct and incorrect first runs in the test period of eighteen days. Similarly the last two columns present the corresponding postoperative scores.

According to the theory of cerebral dominance as applied to intelligent behavior, one might expect a greater reduction in the scores of the group with contralateral lesions, than in the scores of the group with homolateral lesions. This was found not to be the case. Cerebral destructions were followed by an appreciable decrease in the postoperative scores in both groups of rats, but the scores for the two groups are strikingly similar. The average percentage of lesion for the contralateral group was 18.3; for the homolateral group 18.8. On the preoperative tests the groups were again homologous—the contralateral group scoring 75.5 per cent;⁶ the homolateral group 77.7 per cent.⁶ The post-

⁶ Calculated according to Maier (1932a): $\frac{\text{Right minus wrong}}{\text{Total}}$.

TABLE 5

The effect of contralateral and homolateral cerebral lesions on reasoning

NUMBER OF RAT	PERCENTAGE OF LESION	PREOPERATIVE SCORES		POSTOPERATIVE SCORES	
		Correct	Incorrect	Correct	Incorrect
Contralateral lesions					
3	7.6	16	2	15	3
4	7.8	14	4	13	5
5	7.8	14	4	15	3
7	9.6	17	1	16	2
10	12.1	17	1	18	0
12	12.3	15	3	16	2
16	14.7	14	4	17	1
18	15.9	17	1	15	3
20	17.0	17	1	18	0
23	21.3	18	0	15	3
24	21.5	17	1	15	3
25	21.7	16	2	14	4
28	23.0	16	2	14	4
29	23.0	15	3	17	1
32	25.0	17	1	11	7
35	25.1	14	4	11	7
38	25.9	16	2	8	10
40	27.5	15	3	11	7
41	29.2	15	3	12	6
Average....	18.3	15.8	2.2	14.3	3.7
		75.5%		58.9%	
Homolateral lesions					
1	5.5	14	4	15	3
2	6.4	17	1	12	6
6	8.6	17	1	14	4
8	10.5	15	3	15	3
11	12.3	15	3	16	2
14	13.5	15	3	18	0
17	14.9	16	2	17	1
19	16.3	17	1	15	3
21	17.8	15	3	14	4
22	18.7	14	4	10	8
26	21.9	14	4	10	8
27	22.8	18	0	14	4
30	23.3	17	1	16	2
33	25.0	16	2	13	5
34	25.1	18	0	14	4
36	25.4	17	1	14	4
37	25.6	18	0	17	1
39	26.5	15	3	12	6
Average....	18.8	16.0	2.0	14.2	3.8
		77.7%		57.7%	

operative scores for the two groups are 58.9 per cent⁶ for the contralateral group and 57.7 per cent⁶ for the homolateral group. From these results it is clear that there is a reduction in the ability tested following cerebral destruction, but no difference between the results of lesions in the contralateral and those in the homolateral hemispheres.

Conclusions for intelligent behavior

The results of unilateral cerebral destructions clearly indicate that for the function of intelligence in the rat as determined by Maier's reasoning test, there is no evidence for hemispheric cerebral dominance. The results are strikingly in favor of the theory that the hemispheres are equipotential for intelligent behavior in the rat.

DISCUSSION

The foregoing results show that in the rat, as in man, we have three psychological processes which are affected by cortical lesions, namely: (1) the motor function of handedness, (2) the motor response to a visual pattern, and (3) intelligent behavior. The motor function of handedness appears to be localized in a critical area of the anterior portion of the contralateral hemisphere. The visual perceptive process appears less localized, but has been ascribed to the posterior third of the cortex or to the striate area; while intelligent behavior is not localized but is considered a general function of the whole cerebrum.

In man, an exhibition of a dominant hand has been taken to indicate a dominant hemisphere, not only for the motor function of handedness, but for the visual perceptive function and for intelligence. One might assume similarly that since the rat exhibits a definite hand preference it also has a dominant hemisphere for the motor function of handedness, for the visual perceptive process, and for intelligence.

The results of this investigation, however, clearly indicate that in the rat the hemispheres are equipotential for the functions of pattern vision and intelligent behavior even though this animal does exhibit a definite hand preference, and reverses this preference after a cortical lesion in the critical area of the contralateral

hemisphere. It follows, therefore, that the assumption of a dominant hemisphere for the visual function and for intelligent behavior, based on the exhibition of a preferred hand, is unfounded.

For those who propose the theory of hemispheric cerebral dominance in man, we are asking, not that they accept an analogy from rat to man, but that they advance some evidence for the theory other than speculation or interpretation from inadequate clinical data. This experiment indicates that the broad generalizations which have been made concerning the relationship of unilateral cerebral dominance to speech, reading, and writing, are not warranted from merely the determination of the handedness of the subject.

SUMMARY AND CONCLUSIONS

The purpose of this investigation was to furnish experimental evidence in the case of the rat for one or the other of the opposing assumptions: (1) hemispheric cerebral dominance; and (2) hemispheric equipotentiality.

A number of rats were (1) tested for hand preference; (2) trained to react positively to one of a pair of asymmetrical visual patterns (F against mirrored F); and (3) tested for intelligent behavior. The animals were divided into two groups. For those in one group a portion of the cortex was destroyed in the contralateral hemisphere (opposite to the preferred hand), while for those in the other group similar cortical lesions were made in the homolateral hemisphere (same side as the preferred hand). After allowing ten days for postoperative recovery, the animals were again tested for the three functions.

The results of the experiment warrant the following conclusions:

1. Cortical destruction within a critical area of the anterior portion of the contralateral hemisphere changes the hand preference of the rat. A lesion in any portion of the cortex posterior to the critical area of the contralateral hemisphere, or in any portion of the homolateral hemisphere, does not affect the rat's hand preference.

2. The cerebral hemisphere which would be considered "domi-

nant" for handedness (in the conventional use of the term) does not appear to be dominant for the visual function. The results showed that the retention of a motor response to a visual pattern suffered the same loss from a homolateral lesion as from a contralateral lesion. The hemispheres appear to be equipotential for this function. Furthermore there was no indication of a reversed response or "strephosymbolia" following contralateral lesions.

3. There appears to be no evidence for the theory of cerebral dominance as applied to intelligent behavior in the rat as determined by Maier's reasoning test. The results were strikingly in favor of the theory that the hemispheres are equipotential.

4. The results of this investigation are not directly applicable to man. However, the assumption that a preferential use of one hand is an indication of the dominance of one hemisphere for the visual function or for intelligent behavior was not confirmed by our data. On the contrary the results indicate hemispheric equipotentiality. Therefore until some direct experimental evidence is produced which shows the relationships of cortical functioning of handedness and the cortical functionings of other psychological processes which have been attributed to unilateral cerebral dominance, one is warranted in being very skeptical of the theory of hemispheric dominance and its various ramifications in man.

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PLATES I-III

Plates I, II, and III are diagrammatical representations of the extent and locus of cortical lesions. The numbers of the rats and percentages of lesions correspond to the numbers and percentages in the tables. H refers to a homolateral lesion (a lesion on the same side as the preferred hand); and C refers to a contralateral lesion (a lesion on the opposite hemisphere to the preferred hand).

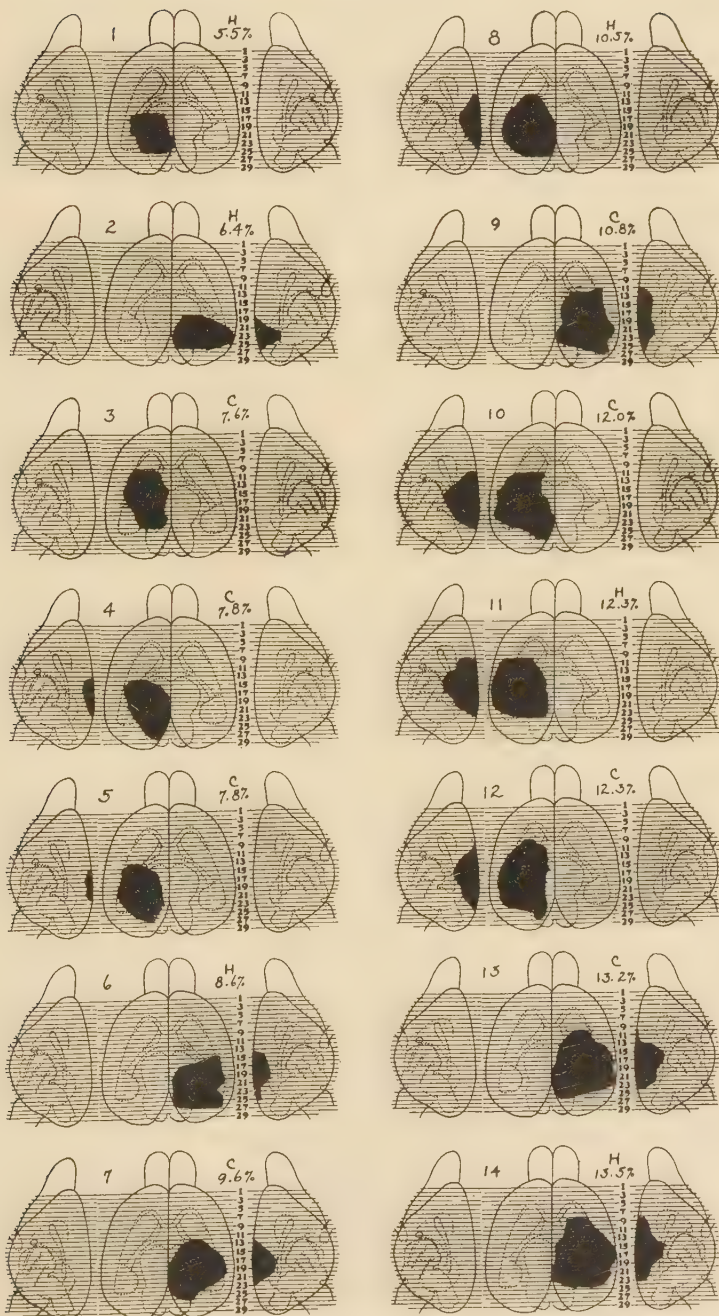


PLATE 1

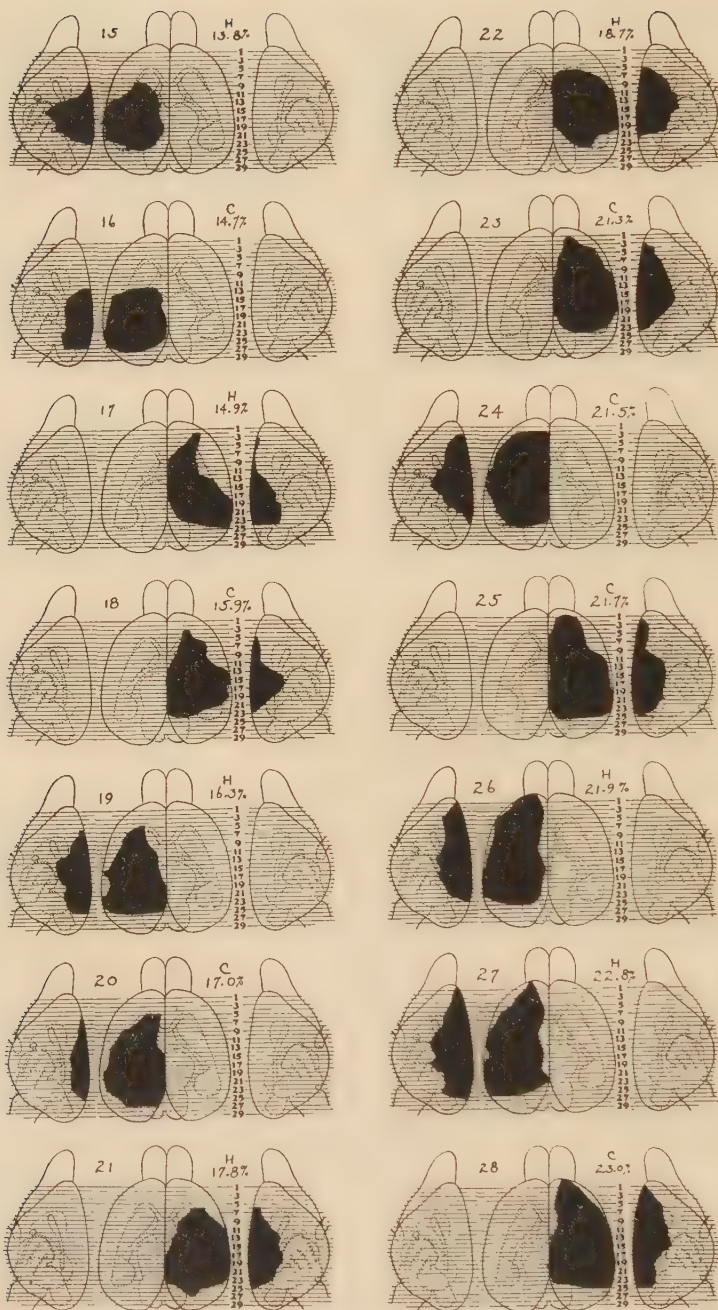


PLATE 2

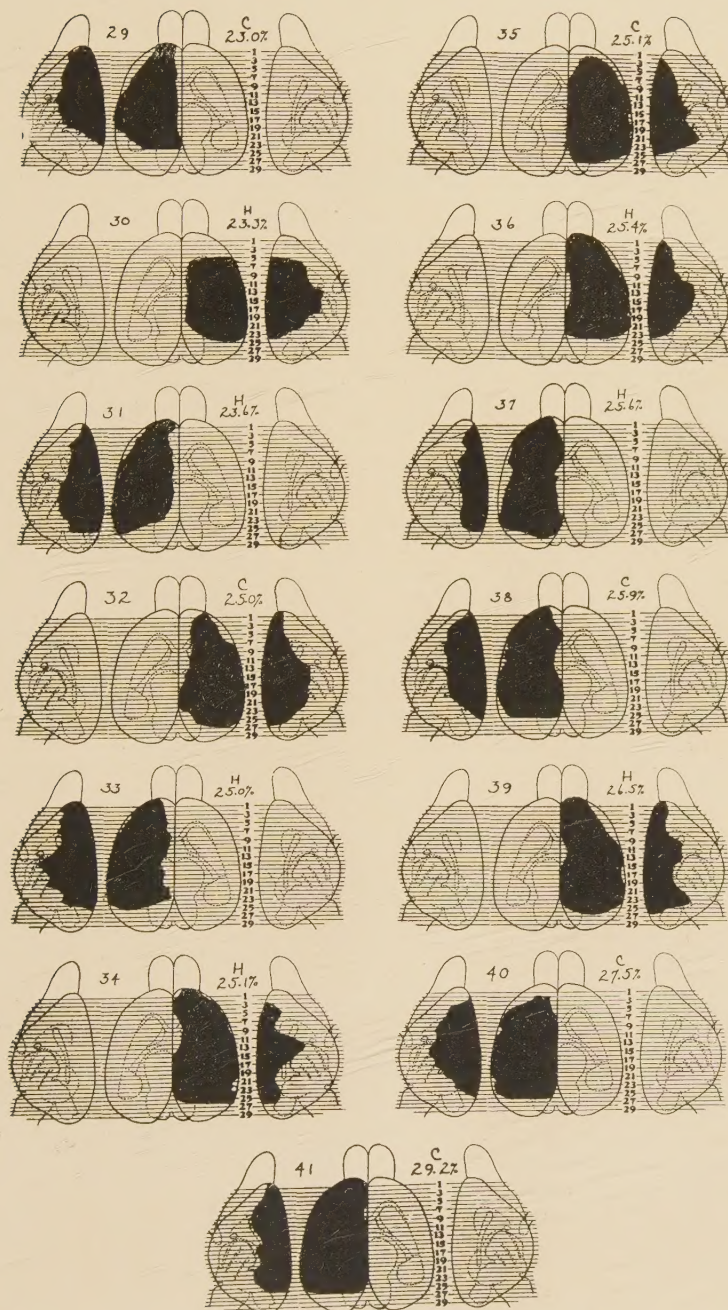


PLATE 3

